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While the genus Phytophthora is not very large, its taxonomy is generally considered to be difficult. From time to time investigators have attempted to overcome this difficulty and to present a simpler scheme of classification. The latest work of this nature is that by Tucker (*9*), who succeeded in bringing together most of the available data on Phytophthora. His own voluminous experiments add much to our knowledge concerning this genus. However, the scheme of classification as proposed by him still leaves room for improvement. Some of the species retained are of doubtful merit; others which he has discarded possess certain claims to recognition; also, certain distinguishing characters proposed by him are not dependable. Such seeming discrepancies are to be ascribed not merely to differences in individual viewpoints but also to the extent and the nature of experimental work employed by each investigator. The writer has maintained that if sufficiently numerous experiments could be made, and if such experiments could be refined enough, probably every isolant of a given species would manifest some distinctive characteristic whereby it could be recognized and separated from every other isolant. However, the problem confronting the taxonomist is not whether such distinctions actually exist or can be demonstrated, but whether a given species actually possesses sufficiently stable characters to remain unaffected, at least for a comparatively long period, by additional strains which come either as new isolants or as new dissociants to tax the elasticity of our species concept.

The genus Phytophthora does not readily lend itself to a natural scheme of classification. Too few morphological distinctions and the too ready tendency of such distinctive lines to overlap have necessitated a more or less arbitrary method of classification. Consequently, there is and perhaps always will be a certain lack of permanency in our keys. As more organisms are studied and more knowledge is accumulated, certain seemingly well-established species may be discarded or new ones established.

The writer believes that there are not more than two or three good species in the genus Phytophthora. However, he realizes that in the light of our present knowledge of biology such a radical view cannot be generally accepted. Consequently he has retained all "species" and "varieties" that can be readily identified by the use of the key given at the

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end of this work. But where confusion is likely to arise, a wholesale elimination of named species has been followed without hesitation. Since taxonomic schemes are or should be prepared not for a few specialists but for the general scientific public, such a course is considered justifiable. The specialist, through constant association, develops a practiced eye that sees many fine distinctions for the expression of which we have no words, and which, therefore, must remain a closed book to the outsider. Consequently what may appear like a true species to the specialist will be nothing more than a source of needless confusion to the average worker.

The experimental work here outlined has been developed to supplement information already available, or to check some results previously obtained. It is believed that there are now sufficient experimental data with which to prepare a working key of simple construction.

TERMINOLOGY

In order to eliminate any possible misunderstanding, some of the more important terms adopted in this work are explained here as follows:

Strain: Any representative of a given species possessing certain distinctive and inherent characteristics whereby it may be separated from every other representative of the same species is termed *strain.* It is unfortunate that this term has been used in literature very loosely and has been applied to any organism regardless of presence or absence of some distinguishing characteristic.

Isolant: This word, rather than *isolate*, has been adopted because it is distinctive, to the point, and free from any possible misunderstanding. The term *isolate* is awkward and may easily lead to confusion. Priority is not sufficient justification for its use.

Dissociation: This term, rather than *mutation* or *saltation*, has been adopted because in the first place it is free from entanglement with genetics, and in the second place it is more expressive of the actual phenomenon. The word *mutation* carries with it a certain degree of permanency and suggests the appearance of something new or some independent entity. The interpretation of the writer does not generally conform itself to such a notion. Dissociation does not usually bring forth and set on their way independent organisms, but merely emerges or submerges the different potentialities of the same organism. Pending the construction of a more expressive term, the word *dissociation* will be used exclusively throughout this paper.

Dissociant: Any sector possessing a sufficient distinction from every other sector, developed in a colony, isolated in pure culture, and perpetuated by constant selection, is termed a *dissociant.* A dissociant, once obtained in pure culture, may revert to the parent form or may further dissociate into some other form, either very rarely or frequently; but so long as it can be maintained in pure culture by constant selection, it is considered a dissociant.

ORGANISMS STUDIED

An attempt was made to secure all the described species of Phytophthora. Three important species, namely, *P. infestans*, *P. thalictri*, and *P. phaseoli*, have been left out of the following list of organisms because we already have sufficient data on these species for an accurate and speedy identification. Certain other species, probably of no taxonomic value, could not be obtained in pure culture from any source; nor do we have full descriptions of them. In so far as the writer is concerned, any organism that has been incompletely described, or is named only provisionally, or cannot be obtained in culture, should be left out of literature. With the exception of the foregoing, therefore, the following list consists of all the species of Phytophthora that have even a slight claim to taxonomic distinction.

TABLE 1—*Organisms used in this work*

Organisms	Received from	Host
P. arecæ (Colem.) Peth. 1	Gadd through Baarn	Areca
P. arecæ 2	National Type Cultures	
	Collection through Baarn	Areca
P. boehmeriæ Sawada	Sawada through Baarn	Boehmeria
P. cactorum (Lib. et Colem) Schroet. 1	Gardner, M. W	Apple fruit
P. cactorum 2	Beach, W. S	Rhubarb
P. cactorum 3	Beach, W. S	Apple fruit
P. cactorum 4	Baarn strain	
P. cactorum 5	Isolated by Leonian	Apple fruit
P. cactorum 6	Rose through Baarn	
P. cactorum 7	v. Luijk through Baarn	Eschscholzia
P. cactorum 8	Baarn	Corylus
P. cactorum 9	Sawada through Baarn	Boehmeria
P. cactorum 10	Peters through Baarn	Cactus
P. cactorum 11	Charles Drechsler	Lilium regale
P. cactorum 12	Charles Drechsler	L. pyrenaicum
P. cactorum 13	Charles Drechsler	L. tenuifolium
P. cactorum 14	Charles Drechsler	L. washingtonium
P. cactorum 15	Charles Drechsler	L. candidum
P. cactorum 16	Charles Drechsler	L. regale
P. cactorum 17	Charles Drechsler	L. speciorum
P. cactorum applanata Chester (1)	Chester, Kenneth S	Lilac
P. cambivora (Petri) Buisman 1	Dufrenoy through Baarn	Castanea
P. cambivora 2	Petri through Holland	Castanea
P. capsici Leonian	Isolated by Leonian	Capsicum
P. cinnamomi Rands 1	Rands	Cinnamomum
P. cinnamomi 2	Tucker, C. M	Persea
P. cinnamomi 3	White, R. P	Rhododendron
P. cinnamomi 5	Blackwell through Baarn	
P. cinnamomi 6	F. P. Mehrlich	Pineapple
P. cinnamomi 7	F. P. Mehrlich	Soil
P. citricola Saw	Sawada through Baarn	Citrus
P. citrophthora (Sm. & Sm.) Leonian 1	H. C. Fawcett	Citrus
P. citrophthora 2	H. C. Fawcett	Citrus
P. citrophthora 3	H. C. Fawcett	Citrus
P. colocasiæ Racib. 1	Schwarz through Baarn	
P. colocasiæ 2	Blackwell through Baarn	
P. cryptogeæ Pethybr	Pethybridge through Baarn	Tomato
P. drechsleri Tucker	Drechsler, Tucker	Potato
P. erythroseptica Pethybr	Pethybridge through Baarn	Potato
P. erythroseptica atropæ Foister	Foister through Baarn	
P. faberi (Faber) Maubl. 1-I	Ashby through Baarn	Cocoa
P. faberi 1-II	Dissociant of 1-I (Leonian)	
P. faberi 1-III	Dissociant of 1-I (Leonian)	
P. faberi 1-IV	Dissociant of 1-I (Leonian)	
P. faberi 1-V	Dissociant of 1-I (Leonian)	
P. faberi 2	Reinking	Cocoa
P. faberi 3	Sundaraman through Baarn	Cocoa
P. faberi 4	Gadd through Baarn	Cocoa
P. heveæ Thompson	Am. Type Culture Collection	Hevea
P. hibernalis Carne	H. C. Fawcett	Citrus
P. hydrophila Curzi	Curzi through Baarn	Capsicum
P. manoana Sideris	Sideris through Baarn	

TABLE 1—(*Continued*)

Organisms	Received from	Host
P. meadii MacRae 1	Thompson through Baarn	Hevea
P. meadii 2	Schwarz through Baarn	Vanilla
P. meadii 3	Baarn	
P. meadii 4	MacRay	Hevea
P. megasperma Drechs. (2)	Charles Drechsler	Hollyhock
P. melongenæ Sawada	Sawada through Baarn	Solanum melongena
P. melongenæ ananaphthoros Sid	Sideris through Baarn	
P. mexicana Hotson et Hartge	Hotson	Tomato
P. nicotianæ v. Breda de Haan 1	Baarn	Tobacco
P. nicotianæ 2	Nolla I strain, Baarn	Tobacco
P. nicotianæ 3	Meurs through Baarn	Tobacco
P. nicotianæ 4	Thompson strain through Baarn	Tobacco
P. parasitica Dast. 1	Welles through Reinking	
P. parasitica 2	Reinking	Citrus
P. parasitica 3	Reinking	Hibiscus
P. parasitica 4	Tucker	Bryophyllum
P. parasitica 5	Reinking	
P. parasitica 6	Isolated by Leonian	Tomato
P. parasitica 7	Reinking	Abaca
P. parasitica 8	Tucker	Tomato
P. parasitica 9		
P. parasitica 10		
P. parasitica 11		
P. parasitica 12	Webber, George	Pepper
P. parasitica 13	Tucker	
P. parasitica 14	Tucker	
P. parasitica 15	Tucker	
P. parasitica 16	Tucker	
P. parasitica 17	Tucker	
P. parasitica 18	Cacao	Hartley
P. parasitica 19	Hibiscus	Reinking
P. parasitica 20	Cacao	Hartley
P. parasitica 21	Taubenhaus	Tomato
P. parasitica rhei Godfrey	Godfrey	Rhubarb
P. parasitica rhei dissociants I to LXXX	Leonian	
P. palmivora Butl. 1	Baarn	
P. palmivora 2	Tucker	Cocoa
P. palmivora 3	Hartley	Borassus
P. palmivora 4	Tucker	Grapefruit
P. palmivora 5	Hartley	Hevea
P. palmivora 6	Ashby through Baarn	
P. porri Foister (3)	C. E. Foister	Leeks
P. pini Leonian	Annie R. Gravatt	Pine roots
P. richardiæ Buisman	Baarn	
P. symmetrica Sid	Sideris through Baarn	
P. syringæ Kleb. 1	Pethybridge through Baarn	Syringa
P. syringæ 2	deBruin through Baarn	Syringa
P. tabaci Saw	Sawada through Baarn	Tobacco
P. terrestris Sherb	Sherbakoff	Tomato

In this list and following tables the organisms are presented under their old names in order to facilitate comparison. In the key at the end of the work are given only those species and varieties which have been retained by the writer.

Arabic numerals accompanying the names of the organisms denote the strain number, while Roman numerals represent the dissociants.

NUTRIENT MEDIA USED

All stock cultures were carried on oatmeal agar in test tubes. For plate cultures, however, the following solid medium was used:

Malt extract	3 grams
Yeast extract	2 grams
Dihydrogen potassium phosphate	0.5 gram
Magnesium sulfate	0.5 gram
Bacto-agar	20 grams
Distilled water	1,000 c.c.

15 c.c. of this agar was used in plates and 10 c.c. in test tubes.

The following nutrient solution was used for liquid cultures:

Proteose peptone	2 grams
Dihydrogen potassium phosphate	0.5 gram
Magnesium sulfate	0.5 gram
Succinic acid	0.2 gram
Dextrose	5 grams
Distilled water	1,000 c.c.

Unless otherwise stated, the foregoing nutrient solution has been used throughout the work, at the rate of 5 c.c. of the solution in each test tube.

TECHNIQUE EMPLOYED

The inoculum-disc technique, as developed by the writer (*4*, p. 761), has been used throughout the experiments. This method insures a uniform quality and quantity of the inoculum. The current practice of jerking out a piece of agar and mycelium from the test-tube cultures and using it as inoculum regardless of its age and size is both inaccurate and misleading. The size and particularly the age of the inoculum may prove very important and may often be controlling factors in subsequent results. Very young growths may often be less resistant to adverse conditions of environment than the older ones. Furthermore, in a cœnocytic fungus like Phytophthora the actual size of the inoculum is of much consequence. The writer (*5*) has demonstrated that even the position of the inoculum and the thickness of agar carried with it often determine its ability to grow or to perish under the influence of unfavorable environments.

EXPERIMENTS

Differential Growth Under the Action of Malachite Green

The writer (*6*) has already shown that different concentrations of malachite green induce an excellent differential growth in fungi, particularly in Phytophthora. He found it desirable, therefore, to repeat the test with all the available cultures of Phytophthora and thus reveal possible specific reactions for use in classification work. Enough of the dye was added to the nutrient solution to yield the following concentrations: 1:2,000,000, 1:3,000,000, 1:4,000,000; 1:8,000,000, and 1:12,000,000. Dissolving the dye in distilled water first and then adding the food ingredients induced the formation of precipitates in case of the higher concentrations of the dye, whereas the addition of the dye directly to the nutrient solution prevented this. Of the solution thus prepared 5 c.c. was placed in each test tube and sterilized at 15 pounds' pressure for 15 minutes. Inoculum discs were cut from the margin of vigorously growing colonies in petri dishes and transferred to the tubes. All aerial mycelium was made to collapse by gently rubbing the platinum needle over the surface of each inoculum before transferring; this prevented the inoculum from floating on the surface of the solution. All inoculum discs were thus made to sink to the bottom of the tube to insure a more

uniform condition. This precaution has been observed wherever nutrient solution was used. After two weeks' incubation at 20° C. the readings were taken.

Comparatively few organisms were able to make any growth in the presence of one part of malachite green in two million parts of the nutrient solution, and in case of many of these the growth was either sparse or erratic; sometimes the fungus was able to grow, and sometimes it failed to do so. In such cases it became necessary to repeat the work several times in order to make sure that a given organism would either consistently fail to grow or else make only an occasional growth. In the latter case the reaction is given as positive despite the occasional or even frequent negative results. When the concentration of a toxic substance lies just at the borderline, inconstant results are to be expected, whereas at more extreme concentrations the results will be either constantly positive or constantly negative; but unless the concentration is higher than any member of the genus will tolerate, one must always look for inconstancy on part of some species or strains. We can no longer admit that all parts of a given colony, or all parts of a given hypha, or even all parts of a given cell are identical. When one inoculum is killed and an adjoining one from the same colony not only fails to die but grows well under identical conditions, we cannot say that the two test tubes filled from the same batch of solution and kept under the same conditions had sufficient differences to yield such extreme results. It is true that many minor differences constantly occur; that no two drops of water are identical; that the solutions in the two test tubes might not be absolutely the same in quality and quantity; that the cotton plugs can never be made identical; etc. Yet it is extremely unreasonable to suppose that such differences can have enough potency to influence life and death. The more outstanding differences that might exist must be looked for in the protoplasm of living things. The numerous and frequent dissociations manifested by many organisms lead to the explanation that the living protoplasm is in a stage of constant flux and that within the protoplasm a given character may be submerged and another one emerged: similarly, ability to resist a given concentration of malachite green may come to the fore in one inoculum and be submerged in another, with the result that one inoculum lives and another dies under the action of that particular concentration of the dye.

The following table gives the results. *0* means no growth; I to V denote the relative abundance of growth. The frequency of Roman numerals signifies the number of times the work was repeated in triplicate cultures. As a matter of fact, many of the organisms were cultured more repeatedly than the table reveals; the data tabulated here represent the average results rather than the total number of replications.

The most striking reaction brought out in the following table is the inability of a number of organisms to grow in the presence of malachite green in such a dilute concentration as one part of the dye to twelve million parts of the nutrient solution. The two strains of *P. cambivora,*

the two strains of *P. colocasiæ*, the single strains of *P. cryptogeæ*, *P. erythroseptica*, *P. erythroseptica atropæ*, *P. richardiæ*, *P. hibernalis*, *P. porri*, and the two strains of *P. syringæ* can immediately be separated from all other organisms in the list.

TABLE 2—*Effect of different concentrations of malachite green on growth of Phytophthoras*

Organisms	1:2,000,000	1:3,000,000	1:4,000,000	1:8,000,000	1:12,000,000
P. arecæ 1	II.O.O.	III.I.III.	III.II.II.	III.III.III.	III.III.
P. arecæ 2	O.O.O.	O.O.O.	O.O.O.	I.O.O.	I.II.I.
P. boehmeriæ	O.O.	O.O.	II.I.O.O.I.	II.II.II.	II.II.
P. cactorum 1	O.O.O.	O.O.O.O.	O.O.	II.II.I.	II.II.
P. cactorum 2	O.O.O.	O.O.O.	O.O.	II.I.I.	II.II.
P. cactorum 3	O.O.O.	O.I.O.	O.O.I.I.	O.II.II.	II.II.O.
P. cactorum 4	O.O.	O.O.	O.O.O.O.	I.O.I.II.	O.I.II.
P. cactorum 5	O.O.	O.O.	O.O.O.O.O.	I.II.II.	II.III.II.
P. cactorum 6	O.O.	O.O.	O.O.O.O.O.	I.I.O.I.I.O.	I.II.II.
P. cactorum 7	O.O.O.	O.O.	II.I.	II.II.	II.II.
P. cactorum 8	O.O.	O.O.	O.O.	II.I.	II.II.II.
P. cactorum 9	O.O.	I.I.	I.I.	II.II.	II.II.
P. cactorum 10	O.O.	O.O.	O.O.	II.II.	II.II.
P. cactorum 11	O.O.	I.I.	I.I.	I.	II.II.
P. cactorum 12	O.O.	O.O.	O.O.	O.O.	II.II.
P. cactorum 13	O.O.	I.I.	I.I.	I.II.	II.II.
P. cactorum 14	O.O.	I.I.	I.I.	II.I.	II.II.
P. cactorum 15	O.O.	O.O.	O.O.	II.I.	II.II.
P. cactorum 16	O.O.	O.O.	O.O.	I.I.	II.II.
P. cactorum 17	O.O.	O.O.	O.O.	I.I.	II.II.
P. cactorum applanata	O.O	O.O	O.O	O.O	II.II.
P. cambivora 1	O.O	O.O.	O.O.O.O.	O.O.O.O.O.	O.O.O.
P. cambivora 2	O.O.	O.O.	O.O.O.O.	O.O.O.O.	O.O.O.
P. capsici	O.O.O.O.	O.O.O.	II.III.II.	III.III.II.	IV.III.IV.
P. cinnamomi 1	O.O.	O.I.I.	O.I.I.I.	O.I.I.II.	II.II.
P. cinnamomi 2	O.O.O.	O.O.O.	O.I.II.	O.II.III.	III.III.
P. cinnamomi 3	O.O.O.	O.O.I.	O.O.I.I.	I.O.II.	O.II.II.
P. cinnamomi 5	O.O.O.	O.O.	O.O.I.I.O.I.	I.I.I.I.	II.II.II.
P. cinnamomi 6	O.O.	O.O.	O.O.	I.II.	II.II.
P. cinnamomi 7	O.O.	O.O.	O.O.I.	II.II.	II.II.
P. citricola	O.O.O.	O.O.O.	O.O.I.II.	II.II.II.	II.III.
P. citrophthora 1	O.O.O.	O.I.O.	II.II.O.	II.II.II.	II.II.II.
P. citrophthora 2	O.O.O.	I.II.O.	II.II.II.	II.II.II.	II.II.II.
P. citrophthora 3	O.O.O.	II.I.I.I.	II.I.	II.II.	III.II.
P. colocasiæ 1	O.O.	O.O.	O.O.O.O.O.	O.O.O.O.	O.O.O.
P. colocasiæ 2	O.O.	O.O.	O.O.O.O.O.	O.O.O.O.	O.O.O.
P. cryptogeæ	O.O.	O.O.	O.O.O.O.	O.O.O.	O.O.
P. drechsleri	O.O.	O.O.	O.O.	I.II.	I.II.
P. erythroseptica	O.O.	O.O.	O.O.O.O.O.	O.O.O.O.	O.O.O.
P. erythroseptica var. *atropæ*	O.O.	O.O.	O.O.O.O.	O.O.O.	O.O.O.
P. faberi 1-I	O.II.O.I.	II.II.II.	I.I.O.II.I.	III.O.I.II.	II.II.II.
P. faberi 1-II	O.II.	I.II.	I.O.I.	I.II.I.	I.II.
P. faberi 1-III	O.O.O.	I.O.I.O.	I.O.I.II.	O.II.II.	II.II.II.
P. faberi 1-IV	O.O.II.O.	O.II.II.	I.O.II.O.	II.III.III.	III.III.III.
P. faberi 1-V	O.O.O.	O.O.	II.I.II.I.	III.II.III.	III.III.
P. faberi 1-VI	O.O.I.	II.I.O.	II.II.II.I.	II.O.II.II.	III.II.
P. faberi 2	O.O.	O.O.	O.O.I.I.	I.O.I.	O.II.II.
P. faberi 3	O.O.	O.O.	O.O.I.O.O.	III.O.O.I.	II.I.O.
P. faberi 4	O.O.	O.O.	O.O.O.O.O.	O.O.O.O.	O.I.O.
P. heveæ	O.O.	O.O.	O.O.	O.O.	I.I.
P. hibernalis	O.O.O.	O.O.O.	O.O.O.	O.O.O.	O.O.O.
P. hydrophila	II.II.II.	II.II.III.	II..II.III.	III.III.III.	III.III.
P. manoana	O.O.	O.O.	O.O.O.I.	O.II.I.	III.III.
P. meadii 1	O.O.	O.O.	O.O.O.O.	O.II.III.III.	III.III.
P. meadii 2	O.O.O.	O.II.II.	II.O.I.II.	II.III.II.O.	II.II.
P. meadii 3	O.O.	O.O.	O.O.O.O.I.	III.III.II.	III.III.
P. meadii 4	O.O.O.	I.II.I.	I.O.II.II.	II.III.III.	III.III.
P. megasperma	O.O.	O.O.	O.O.	O.O.	I.I.
P. melongenæ	I.I.	I.I.	I.II.II.	II.II.	II.II.II.
P. melongenæ var. *ananaphthoros*	O.I.	I.I.	O.I.O.II.II.	II.II.	II.II.II.
P. mexicana	O.O.II.III.O.	III.III.	III.IV.IV.	IV.IV.	V.IV.
P. nicotianæ 1	I.II.	I.II.II.	I.II.I.	II.I.II.	II.II.
P. nicotianæ 2	O.I.	I.II.	I.II.II.	II.II.II.	II.II.
P. nicotianæ 3	II.I.O.	II.II.II.	I.II.II.	II.II.II.	II.III.
P. parasitica 1	O.O.	O.O.	O.O.O.O.O.	II.I.O.III.	II.III.III.
P. parasitica 2	O.O.	I.I.I.	I.O.I.	II.II.II.	II.III.

TABLE 2—(*Continued*)

Organisms	1:2,000,000	1:3,000,000	1:4,000,000	1:8,000,000	1:12,000,000
P. parasitica 3	0.0.	0.0.	0.0.0.0.	III.0.III.	III.0.
P. parasitica 4	I.I.II.	II.II.II.	0.0.II.	II.I.II.	II.II.
P. parasitica 5	0.I.0.0.	I.I.0.	0.0.I.	II.II.II.	II.II.
P. parasitica 6	0.0.0.	I.II.II.	I.I.II.	II.II.II.	II III
P. parasitica 7	0.0.0.	0.I.0.	II.0.II.	III.II.II.	II.II.
P. parasitica 8	I.I.0.	I.II.I.	I.I.I.	II.II.II.	II.II.
P. parasitica 9	0.II.0.	I.II 0.I.	I.0.I.I.	II.II.II	II.II.
P. parasitica 10	0.0.0.	I.I.II.	II.0.0.	III.II.III.	III.V.
P. parasitica 11	0.0.	0.0.	II.0.II.I.	II.II.	II.II.
P. parasitica 12	II.0.II.	III.III.III.	II.III.0.III.	III.IV.IV.	IV.IV.
P. parasitica 13	II.I.II.	II.II.II.	I.II.II.	II.II.II.	II.II.
P. parasitica 14	0.0.I.0.	0.II.I.	II I.I.	I.0.I.	II.II.
P. parasitica 15	0.0.0.	II.II.I.	I.II.I.	II.II.II.	II.II.II.
P. parasitica 16	0.I.I.	II.I.I.	I.II.I.	II.II.II.	II.II.II.
P. parasitica 17	I.II.II.	II.II.II.	II.II.II.	II.II.II.	II.II.
P. parasitica 18	I.I.0.	0.I.0.	II.II.II.	II.II.II.	II.II.
P. parasitica 19	I.II.I.0.	I.0.I.	II.II.II.	I.II.I.	II.II.
P. parasitica 20	0.0.	0.0.	0.0.0.0.	0.I.I.	I.II.II.
P. parasitica 21	III.III.III.	III.IV.III.	IV.IV.	IV.IV.IV.	IV.IV.IV.
P. palmivora 1	0.0.	0.0.	0.0.0.0.	0.II.I.	II.II.
P. palmivora 2	0.0.	0.0.	0.0.0.0.I.	0.0.III.0.	0.III.0.
P. palmivora 3	0.0.	0.0.	0.0.0.0.0.	0.0.0.0.	0.I.II.0.
P. palmivora 4	0.0.	0.0.	0.0.I.I.	0.III.II.	V.III.
P. palmivora 5	0.0.	0.0.	0.0.0.0.II.	III.0.II.	0.III.II.
P. palmivora 6	0.0.	0.0.	0.0.0.0.0.	0.0.II.	II.II.
P. pini	0.0.0.	0.0.0.	0.0.0.I.I.0.	I.0.II.II.	II.0.II.II.II.
P. porri	0.0.0.	0.0.0.	0.0.0.	0.0.	0.0.
P. richardiæ	0.0.0.	0.0.0.	0.0.0.0.	0.0.0.0.	0.0.0.
P. symmetrica	0.0.I.II.	II.I.0.II.	0.II.III.II.	0.IV.V.	IV.V.V.
P. syringæ 1	0.0.0.	0.0.0.	0.0.0.	0.0.0.	0.0.0.
P. syringæ 2	0.0.0.	0.0.0.	0.0.0.	0.0.0.	0.0.0.
P. tabaci	0.0.	0.0.	0.0.0.0.I.	II.II.II.	II.III.II.
P. terrestris	I.0.0.	I.0.0.	I.I.II.I.	II.II.II.	II.II.II.

Going to the highest concentration of malachite green, we find very few organisms which were able to make any growth, as follows: *P. arecæ 1, P. faberi* 1-I, 1-II, 1-IV, and 1-VI, *P. hydrophila, P. mexicanæ, P. nicotianæ* 1, 2, and 3, *P. parasitica* 4, 5, 8, 9, 12, 13, 14, 16, 17, 18, 19, and 21, *P. symmetrica,* and *P. terrestris.* The results are not significant enough to be used in classification; they merely indicate the limits of variability which some organisms can attain.

In the presence of 1:3 million parts of the dye the following organisms made some growth: *P. cactorum* 3, 9, 11, 13, and 14 were able to tolerate the dye at this concentration, whereas the remaining twelve failed to do so, thus illustrating the all too common but less appreciated interstrainal differences. *P. capsici, P. cinnamomi* 1 and 3, all three strains of *P. citrophthora,* all strains of *P. faberi* 1 except 1-V, *P. meadii* 1 and 4, *P. melongenæ,* P. *melongenæ ananaphthoros,* all three strains of *P. nicotianæ,* all strains of *P. parasitica* except 1, 3, 11, and 20, *P. symmetrica,* and *P. terrestris* grew, at some time or another, in the presence of 1:3 million parts of the dye.

The dissociants of *P. parasitica* var. *rhei* were by no means identical in their reaction towards the dye. While all grew in the presence of 1:8 and 1:12 million concentrations of malachite green, they were decidedly erratic when higher concentrations were used. Only a few of them could tolerate 1:2 million parts of malachite green, but only thirteen failed to grow in 1:3 million parts of the dye. This, together with the data tabulated above, shows that in so far as the *P. parasitica* group of organisms

is concerned, the use of malachite green is not a satisfactory means of bringing about a dependable segregation.

Differential Growth Under the Influence of Temperature

Temperature relationships have been extensively used by systematists and pathologists as reliable criteria in biological work; yet a great many discrepancies exist in the data submitted by different workers. It is a well-known fact that the nature of the substratum exerts a great influence upon the ability of a given organism to resist the effect of lethal degrees of temperature, particularly where the limits of temperature tolerance are rather narrow. It is very unfortunate that we do not have a standardized medium or sets of such media to be used in comparative work. With organisms like Phytophthora, where organic nitrogen is essential for good growth, the use of inorganic nitrogen in the medium would be out of question. The next best thing, however, is to use such standardized substances as malt extract and yeast extract, which are obtained readily enough and which form a clear agar conducive to an easy detection of the minutest amounts of growth. The malt extract-yeast extract agar, as previously described in this paper, has been used in these temperature studies. In addition, the experiment was repeated with the proteose-peptone nutrient solution; this served as an effective check to assure that the adsorption factor, which is prominent in case of agar slants at high and at very low temperatures, did not affect the results.

Temperature variations in different types of incubators are also factors of considerable importance and may mean the difference between growth and no growth. In his work with the effect of temperatures upon Phytophthora species Tucker (*loc. cit.*) states that "the variation in temperature did not exceed about 1.5° C." This variation is considerable and cannot help but lead to less dependable results. In the writer's work

TABLE 3—*Effect of temperature on growth of Phytophthoras*

Organisms	8° C.	31° C.	35° C.	37° C.
P. arecæ 1	II.O.O.I.O.II.I.	III.III.	I.II.I.	O.O.
P. arecæ 2	O.O.O.O.O.O.	II.II.	O.O.O.O.	O.O.
P. boehmeriæ	I.I.O.O.O.	II.II.	O.O.O.	O.O.
P. cactorum 1	I.II.II.II.	II.I.	O.O.O.	O.O.
P. cactorum 2	II.II.III.II.	I.I.	O.O.O.	O.O.
P. cactorum 3	III.II.II.	I.I.	O.O.O.	O.O.
P. cactorum 4	III.II.II.	O.O.	O.O.O.	O.O.
P. cactorum 5	III.II.II.	I.I.	O.O.O.	O.O.
P. cactorum 6	III.III.II.	I.I.	O.O.O.	O.O.
P. cactorum 7	O.O.	II.II.	O.O.	O.O.
P. cactorum 8	II.II.	I.II.	O.O.	O.O.
P. cactorum 9	O.O.	I.I.	O.O.	O.O.
P. cactorum 10	O.O.	I.II.	O.O.	O.O.
P. cactorum 11	III.III.	II.II.	O.O.	O.O.
p. cactorum 12	II.III.	II.III.	O.O.	O.O.
P. cactorum 13	II.II.	III.II.	O.O.	O.O.
P. cactorum 14	II.III.	II.II.	O.O	O.O.
P. cactorum 15	III.III.	III.II.	O.O.	O.O.
P. cactorum 16	II.II.	III.IV.	O.O.	O.O.
P. cactorum 17	II II.	II.II.	O.O.	O.O.
P. cactorum var. *applanata*	O O.	II.II.	O.O.	O.O.
P. cambivora 1	O.III.II.	III.II.	O.O.O.	O.O.
P. cambivora 2	II.II.II.	III.II.	O.I.I.O.	O.O.

TABLE 3—(*Continued*)

Organisms	8° C.	31° C.	35° C.	37° C.
P. capsici	O.O.	III.IV.	II III	O.O.
P. cinnamomi 1	O.II II I.	IV II.	O.O.O.	O O.
P. cinnamomi 2	I.O I I.O.	III II.	O.O.O.	O.O.
P. cinnamomi 3	I.II.II.I	III.II.	O.O.O O.	O O.
P. cinnamomi 5	O.I II.II.I	V.III.	O.O O O.	O O.
P. cinnamomi 6	II.II.	III II.	O I O I.	O.O.
P. cinnamomi 7	II II.	III.II.	O.I I O.	O.O.
P. citricola	III.III.III.	O.O.	O.O.O	O.O.
P. citrophthora 1	II.III.II.	II.I.	O.O.O.	O.O.
P. citrophthora 2	II.II II.	II.I	O.O.O.	O.O.
P. citrophthora 3	I.I I.	III.IV.	III III.III	I.II.
P. colocasiæ 1	O.O.O.	I.II.II.	O.O.O.	O.O.
P. colocasiæ 2	O.O O.	IV.II	O.O O	O.O.
P. cryptogeæ	IV.III.II.	V II.	O.O.O.	O.O.
P. drechsleri	III II.	III.III.	IV.IV.	II.II.
P. erythroseptica	II.III III.	I.I.II.	O.O.O.	O.O.
P. erythroseptica var. *atropæ*	III.III.III.	O.I.O.I	O.O.O.	O.O.
P. faberi 1-I	I II I.O.	III.IV.III.	III.IV.	II.II.
P. faberi 1-II	O.O.O.O.	III.IV.	III.III.III	I.I.
P. faberi 1-III	O.O.O.O.	II.II.	I.I O.O.	I.O.
P. faberi 1-IV	II.I.I.O.	IV.III.	III.III.III.	I.I.
P. faberi 1-V	O.O.O.O.	II.II.	O.O.O.	O.O.
P. faberi 1-VI	O.O.O.	III.III.	II II.II	I.O.
P. faberi 2	O.O.O.	IV.II.	O O.O.O.	O.O.
P. faberi 3	O.O.O	II.II.	O.I.II.	O.O.
P. faberi 4	I I O.O.O.	II.II.	I.I.I.	O.O.
P. hevew	O.O O.	I.I.	O.O.	O.O.
P. hibernalis	III III.	O.O	O O.O.	O.O.
P. hydraphila	O.II.I.	II.III.	II II.I.III.	I.I.
P. manoana	O.O.O.O.	II.III.	II.I I.O.	O.O.
P. meadii 1	II.II.O.II.	V.IV.	O O O O.	O.O.
P. meadii 2	II I I	IV.III.	O.O.O O.	O.O.
P. meadii 3	II.II.II.	V V.	O.O.O.O.	O.O.
P. meadii 4	O.O.O.	III.II.	O O O.O.	O.O.
P. megasperma	III.II.	I.I.	O.O.	O.O.
P. melongenæ	O.O.O.O.	III.IV.	II.III III.	I.II.
P. melongenæ var. *ananaphthoros*	I.I I.I.	IV.IV.	III.II.III.	I.II.
P. mexicana	I I I.I.	IV.III.	III.III.III.	I.O.
P. nicotianæ 1	I I.O.O.I	IV.IV.	III.II.III.	I.I.
P. nicotianæ 2	O.O.O.O.	IV.IV.	III.II.III.IV.	I.I.
P. nicotianæ 3	II.II.II.I.	IV.III.	III.III.III.	I.I.
P. parasitica 1	O O.O.O.	III.III.	O.O.I.	O.O.
P. parasitica 2	I.I O.O.O.	III.IV.	II.II.II.	O.O.
P. parasitica 3	O.O.O.O.	III.II.	I I I.	I.O.
P. parasitica 4	I I.O.	III.III.	II II.	I.I.
P. parasitica 5	I I.O.O.	III.IV.	II.II.II.	I.I.
P. parasitica 6	O.O.I.O.	IV.III.	II II.II.	O.O.
P. parasitica 7	O.O.O.O.	IV.III.	II II.II.	I.I.
P. parasitica 8	O.O.I.I.	III.IV.	II.II.	I.I.
P. parasitica 9	I.I.O.I.	III.III.	II.II.II.IV.	I.I.
P. parasitica 10	I.I.O.I.I.	III.IV.	II.II.II.	I.I.
P. parasitica 11	I I.I.O.	IV.III.	II.II.II.	O.O.
P. parasitica 12	II.II.I.O.	III.III.	I.II.I.	I.O.
P. parasitica 13	I.O.O.O.	III.IV.	II.II.I.II.	I.I.
P. parasitica 14	I.I.O.O.O.	II.O.I.	O.O.O.O.	O.O.
P. parasitica 15	I.I.I.II.O.	III.III.	II.II.II.O.O.	I.I.
P. parasitica 16	II.I.II.I.	III.III.	III.III.II.II.	I.I.
P. parasitica 17	I.I.I.I.O.	III.III.	III.II IV.III.	I.I.
P. parasitica 18	O O.O.O.	III.IV.	II.II.III.III.	I.I.
P. parasitica 19	I.I.O.I.O.	III.IV.	II.II.II.III.	I.I.
P. parasitica 20	O O.O.O.O.	III.IV.	O.I.O.O.	O.O.
P. parasitica 21	II.I.II.	III.IV.	III.II.III.II.	I.O.
P. palmivora 1	O.O.O.O.	II.II.	I.I.I	O.O.
P. palmivora 2	I.I.I.I.	V.III.	O.O.I.	O.O.
P. palmivora 3	O.O O.O.	III II.	II.I I.O.	O.O.
P. palmivora 4	O O.O.O.	III.III.	O.O.I.O.	O.O.
P. palmivora 5	I I.O.I.O.	V.V.	O.O.O.O.	O.O.
P. palmivora 6	O O.O.O.	II.II.	I.I I.O.	O.O.
P. pini	III.II III.III.	I.I.	O.O.O.	O.O.
P. porri	II II	O.O.O.	O.O.	O.O.
P. richardiæ	I.III.II.O.	O.O.O.	O.O.O.	O.O.
P. symmetrica	III.III.I.O.	II.III.	II.II.III.III.	I.I..
P. syringæ 1	I.O.II.II.II.	O.O.	O.O.O.	O.O.
P. syringæ 2	II.II.	O.O.	O.O.	O.O
P. tabaci	O.O.O.O.	III.III.	II.II.III.IV	I.O
P. terrestris	I.I.O.O	IV.IV.	III.II.III.III.	I.I.

the fluctuation was only about two tenths of one degree. All cultures were made in duplicate and the work was repeated several times in order to approach the limits of variability of each individual organism. The readings were taken after an incubation of two weeks. (See Table 3.)

The foregoing table shows that only a few organisms were able to grow at 37° C. *P. citrophthora* 3, *P. drechsleri*, all the dissociants of *P. faberi* 1 except V, *P. hydrophila*, *P. melongenæ*, *P. melongenæ* var. *ananaphthoros*, *P. mexicana*, the three strains of *P. nicotianæ*, *P. parasitica* (15 of the 21 strains), *P. symmetrica*, *P. tabaci*, and *P. terrestris* were able, at one time or another, to make from slight to fair growth at this high temperature. At 35° C. a comparatively large number of organisms grew. The uniformity of all strains of *P. cactorum* in their failure to grow at this temperature is at once noticeable. On the other hand, *P. arecæ* 1 grew and *P. arecæ* 2 failed to grow; *P. cambivora* 1 did not grow, *P. cambivora* 2 did. Only two of the six strains of *P. cinnamomi* were able to make a slight and sporadic growth. Of the three strains of *P. citrophthora* two made no growth and one did; two strains of *P. faberi* grew and two failed to do so; only one strain of *P. parasitica* consistently failed to grow. The same applies to *P. palmivora*. Only very few organisms failed to make any growth at 31° C., as follows: *P. cactorum* 4, *P. citricola*, *P. hibernalis*, *P. porri*, *P. richardiæ*, and the two strains of *P. syringæ*. In order further to differentiate between these, an additional temperature, 27° C., was used. *P. hibernalis*, *P. syringæ*, and *P. porri* made no growth, and when after an exposure of six days these cultures were transferred to 20°C., the first two showed no sign of life, while *P. porri* began to grow and form a colony. Thus the value of temperature, in so far as the available and known strains of these species are concerned, becomes decidedly a limiting factor in taxonomy.

The lowest temperature used in these experiments, 8° C., did not yield very many clear-cut differentiations. The following organisms failed to make any growth at 8° C.: *P. arecæ* 2, *P. cactorum* 7, 9, 10, *P. cactorum* var. *applanata*, *P. capsici*, *P. colocasiæ* 1, 2, *P. faberi* 1-II, 1-III, 1-V, 1-VI, *P. faberi* 2, 3, *P. heveæ*, *P. manoana*, *P. meadii* 4, *P. melongenæ*, *P. nicotianæ* 2, *P. parasitica* 1, 3, 7, 18, 20, *P. palmivora* 1, 3, 4, 6, and *P. tabaci*. However, it should be noted that this temperature serves to separate *P. erythroseptica* from *P. heveæ*, and *P. colocasiæ* from *P. cambivora* and *P. erythroseptica* var. *atropæ*.

If we now refer to the dissociants of *P. parasitica rhei*, we find plenty of support for the assertion that the *P. parasitica* group cannot be classified by the use of temperature responses:

Ninety dissociants developed from a single sporangium culture of *P. parasitica* var. *rhei* were subjected to the effect of 8° C., 27° C., 31° C., 32.5° C., and 35 °C. All these failed to grow at 8° C.: all grew at 27° C.; twelve dissociants failed to grow at 31° C.; 23 failed to grow at 32.5° C., and 61 made no growth at 35° C. Such a behavior seems remarkable; yet the dissociants of this one strain are merely repeating the behavior of the different strains of the species and lend support to the writer's theory that dissociants trace the variability of the species. If the different

strains of a given species are capable of showing wide temperature tolerances, why should the dissociants of the strain not do the same? This seemingly erratic but highly normal behavior is to be noted in connection with every experiment.

Production of Sporangia and Oogonia in Distilled Water

The ability to form sporangia, and particularly oogonia, in distilled water is a dependable specific character. Many species and strains reproduce themselves very readily on such media as oatmeal agar and cornmeal agar; but once the source of food is removed, a number of them will remain sterile and only a few species will give rise to sexual bodies.

In this experiment pea broth was used as the nutrient medium. Where it is desirable to wash a well-grown mycelium free from food, a comparatively clear liquid, as free from starch grains as possible, becomes a necessity. Mature peas will not serve the purpose; one must, therefore, have soft, green peas. Canned peas are best, No. 1 size wrinkled peas being ideal.

TABLE 4—*Reproduction by well-nourished mycelium in distilled water*

Both oogonia and sporangia, or only oogonia formed	Only sporangia or sporangia and chlamydospores formed	Neither sporangia nor oogonia formed, but only chlamydospores
P. boehmeriæ	*P. arecæ* 1 and 2	
P. cactorum (all strains)	*P. cambivora*	
	P. capsici	
P. catcorum var. *applanata*	*P. citrophthora* 1 to 3	*P. cinnamomi* (all strains)
P. citricola	*P. colocasiæ* 1 and 2	
P. cryptogeæ	*P. erythroseptica* var. *atropæ*	
P. erythroseptica	*P. fabria* (all strains)	
P. heveæ	*P. hydrophila*	
P. hibernalis	*P. manoana*	
P. megasperma	*P. meadii* 1 to 4	
P. richardiæ	*P. melongenæ*	
P. pini	*P. melongenæ* var. *ananaphthoros*	
	P. mexicana	
	P. nicotianæ 1, 2	
	P. parasitica (all strains)	
	P. palmivora (all strains)	
	P. symmetrica	
	P. syringæ 1, 2	
	P. tabaci	
	P. terrestris	

The contents of one can (1 lb. 4 oz.) were thoroughly mashed and enough distilled water was added to yield 4,000 c.c. of the liquid. This was brought to boil and was then allowed to settle. The heavier masses and most of the starch were left behind and the comparatively clear liquid was siphoned off. By passing this through absorbent cotton, more of the suspended material was eliminated from the liquid. The liquid was then placed in flasks and sterilized. Approximately 75 c.c. of this medium was then placed in glass-covered and hot-air-sterilized dishes of 100 c.c. capacity (preparation dishes); each dish was inoculated with four or five bits of mycelium from the stock culture. These were allowed to grow until some vigorous colonies were formed. Usually 3 to 4 days' incubation at 20-25° C. will be sufficient to induce the desired amount of vegetative growth before reproduction begins. By means of flamed forceps these colonies were then transferred to another series of dishes con-

taining sterilized distilled water and were washed by gently shaking them with a rotary motion. After washing in three changes of water, the mycelium was transferred to a smaller sterilized preparation dish, the bottom of which was barely covered with a thin layer of sterilized distilled water. The dishes thus prepared were kept at 20° C. for three days and were then examined for sporangia and oogonia. Table 4 gives the results.

Three sharply defined groups are brought out from the foregoing experiments, with a remarkable absence of overlapping.

The same uniformity is found in all the dissociants of *P. parasitica rhei*. In only three dissociants was sporangium production scanty; but this was compensated by an abundant production of chlamydospores. When the most cosmopolitan and variable group of Phytophthora like *P. parasitica* manifests such an unusual uniformity, it speaks well of the dependability of the test.

Some of the organisms which failed to produce sexual bodies in distilled water, regularly form them in such substrata as oatmeal agar and cornmeal agar. This, however, is not a sufficiently dependable character in its regularity, particularly in the *P. parasitica* and *P. palmivora* groups, to serve as an unerring guide in taxonomy. The writer (7) and others have demonstrated heterothallism in *P. parasitica*. Heterothallism, however, is not a constant and dependable phenomenon. The writer (*loc. cit.*) has shown that there are homothallic, heterothallic, and neutral strains in *P. parasitica*, *P. palmivora*, *P. faberi*, and others; that some will at one time function as heterothallic and at other times homothallic organisms, and that sex reversal may also take place as a result of dissociation. In such cases sexuality becomes relative in its importance. It is quite probable that most if not all of the so-called heterothallic strains are also homothallic, except that the tendency towards maleness and femaleness may, at times, come to the fore. Similarly, sexually neutral and sexually active phases may be in the same dependent relation towards each other, the one or the other being emerged and submerged. After all, the ability to give rise to sexual bodies is no more fundamental than the ability to tolerate certain adverse environmental conditions. If the same organism may at one time grow and at another time be killed under the same adverse condition because of a peculiar shuffling of protoplasmic properties, there is no reason why sexuality should form an exception. However, the writer does not wish to convey the impression that such things are universal. Some of these organisms are remarkably stable in many of their behaviors. The *P. cactorum* group has not at all varied in regard to its sexuality. All the 90 dissociants of *P. parasitica rhei* have remained either homothallic or neutral, and no matter in what combinations they were mated with known heterothallic strains, they remained unaffected, the neutrals remaining as neutrals and the homothallic strains continuing to remain homothallic. The latter, however, have shown a strong tendency towards parthenogenicity. Comparatively few antheridia form, and the oogonia develop without being accompanied by male bodies. These parthenogenetic bodies are not at all to be con-

fused with chlamydospores. The latter are very large, irregular-sized bodies without any differentiation of their protoplasm and without pigment, whereas parthenogenetic oogonia show a double wall and a distinct ooplasm, and upon maturity become decidedly deep golden brown in color.

Differential Growth Under the Action of Tartaric Acid

In these experiments two concentrations of tartaric acid, 0.1 and 0.2 percent, were used in the nutrient solution. Despite the fact that the work was repeated at least a dozen times, each time in triplicate cultures, the results have been so inconstant that but slight value can be attached to the data obtained. The following were the only organisms capable of making a fairly consistent growth in the presence of 0.1 percent tartaric acid:

P. arecæ 1 and 2
P. cactorum 2, 3, and 7
P. cinnamomi, all strains
P. citricola
P. cryptogea
P. drechsleri
P. faberi 1-I, 1-II, and 4
P. heveæ
P. hydrophila
P. megasperma
P. melongenæ
P. melongenæ var. *ananaphthoros*
P. nicotianæ, all strains
P. palmivora 5
P. richardiæ
P. terrestris

The higher amount of tartaric acid induced such slight and erratic growth in the few organisms which tolerated this concentration that it is not given here.

In terms of pH, a nutrient solution containing 0.1 percent tartaric acid gives a reading of 3.0, after sterilization in the autoclave. The behavior of all strains of *P. cinnamomi* has been remarkably uniform throughout the experiments. Of all the 90 dissociants of *P. parasitica* var. *rhei* 56 grew and the remaining 34 failed to grow in the presence of 0.1 percent tartaric acid in the nutrient solution. It is concluded that in so far as this acid is concerned, it cannot induce dependable differential growth in Phytophthora species.

Hydrochloric acid was also tested but it yielded no more constant results than did tartaric acid.

Differential Growth Induced by Potassium Carbonate

Instead of the nutrient solution, which is quite acid, bacto-dextrose-broth was used in this test. This gives a final reading of pH 6.7 and is,

therefore, a better medium for the purpose of this experiment. Anhydrous potassium carbonate, in concentration of 0.25 per cent, was added to the broth. Five c.c. of the solution was then poured in each test tube and sterilized at 15 pounds' pressure for 15 minutes. The following organisms showed growth:

P. boehmeriæ
P. cambivora 1 and 2
P. cactorum 4, 11, 16
P. erythroseptica
P. faberi 1-III, 2, 3, 4
P. hibernalis
P. megasperma
P. melongenæ var. *ananaphthoros*
P. nicotianæ 4
P. parasitica 3, 4, 13, 18
P. pini
P. richardiæ

The foregoing results, like those obtained with tartaric acid, are considered neither significant nor reliable enough to be used in taxonomic work.

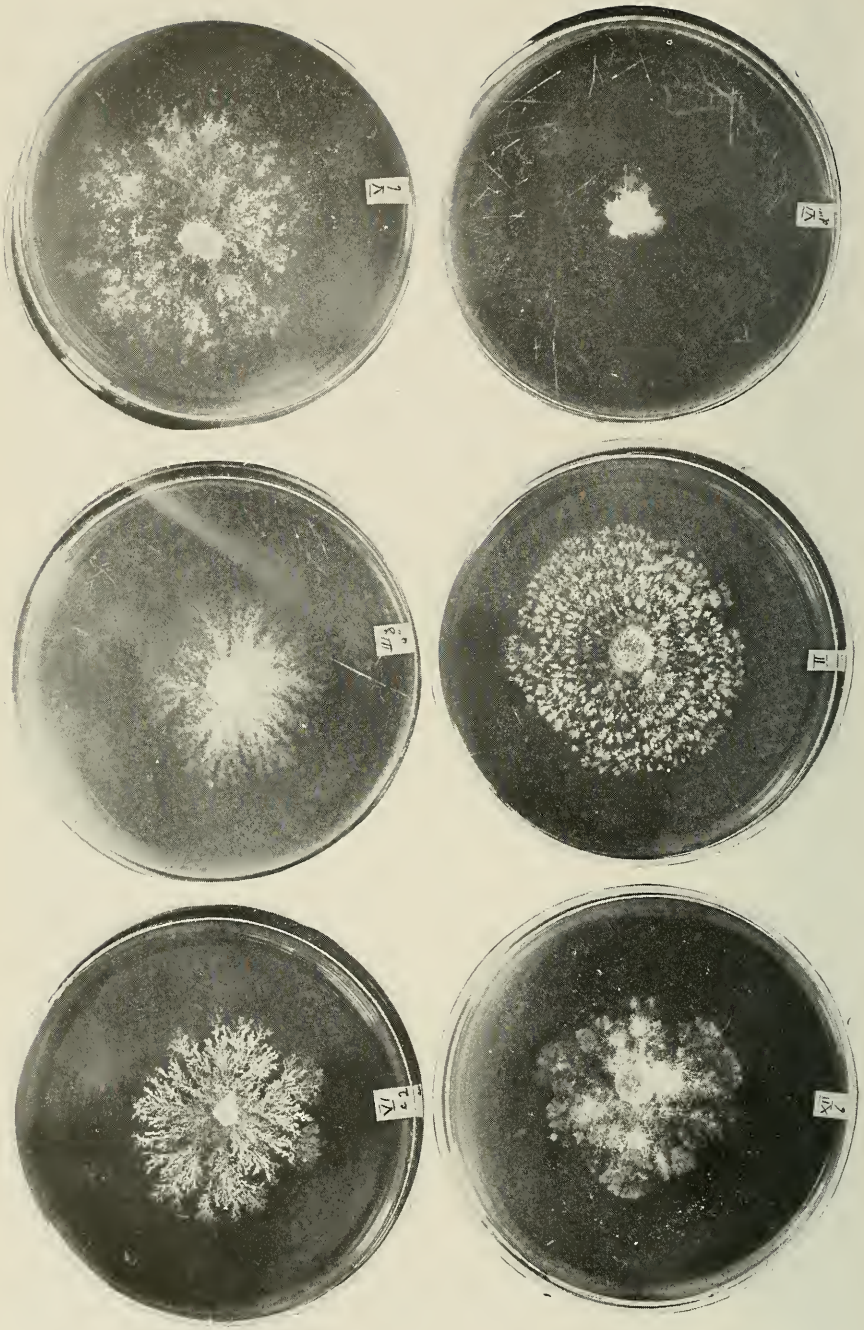
DISCUSSION

A given species of Phytophthora, as conceived by the writer, is not an absolute entity, permanently and definitely established in the scheme of things, but a fluctuating group of organisms more or less loosely bound in a flexible orbit. It is therefore unwise to regard any species as firmly fixed. Only a few years ago *P. palmivora, P. faberi, P. arecæ,* and *P. meadii* were considered by nearly all mycologists to be well-defined and readily recognizable species, and the writer's earlier proposal to combine them into one was not generally accepted. But in the light of further studies these are all recognized now as one, and no one disputes the wisdom of the combination. Similarly, the writer's proposal to combine *P. fagi* with *P. cactorum* was frowned upon, but a few years later the merger was accomplished without any protest. When the writer described *P. pini* as a new species, he had no other recourse because the nature of experiments under which this and other organisms were studied at that time made it behave as a different organism from *P. cactorum.* The rate of its growth was twice as rapid as that of any other strain of *P. cactorum* available at that time; it produced both paragynous and amphigynous antheridia, often both types on the same oogonium; unlike *P. cactorum* it formed its sexual bodies under a great many different conditions. However, under the experiments outlined in this paper where the procedure is materially altered, *P. pini* and *P. cactorum* show identical reactions; furthermore, additional strains of *P. cactorum* now available produce more rapidly spreading colonies than the older ones, and while the writer has not observed any oogonia of *P. cactorum* with a number of

antheridia attached, this is not a character specific enough to justify the retention of *P. pini*. The writer agrees with Tucker that *P. pini* and *P. cactorum* are the same thing. Many other cases of similar nature might be cited, but the foregoing are sufficient to show that the species has only a relative stability. It is doubtful if any species will "stay put." Living things are too plastic to conform to the preconceived notions of the taxonomist and to remain immutable. Changes occur under the very eye of the investigator; gradual or even sudden progressions continue to push out a given organism until it can no longer be contained within its former specific orbit, making it necessary for us either to change our concept or to recognize such departures as the beginnings of new species. After all, even a concept cannot be indefinitely stretched; otherwise it will become a confusing mass. The ideal procedure is one where extremes are avoided and where neither a multiplicity of species nor an overcrowded species concept may result. Such a procedure is attempted in this work; any organism that can easily be distinguished from any other organism with which it is closely allied is retained here under whatever name it happens to possess, but where sharply defined and easily recognized characters are lacking, the retention of the specific rank is considered unwise.

The degree of cosmopolitanism often runs in parallel lines with the degree of variability of Phytophthora species. This is particularly applicable where heterothallic tendencies are to be found. *P. cactorum* is omnivorous and cosmopolitan, yet it constitutes a fairly stable group of fungi. While *P. pini* and *P. cactorum applanata* manifest certain sharp departures from the type, such departures are not yet of sufficient significance to disturb the specific orbit. On the other hand the *P. parasitica* and *P. palmivora* group of organisms, where the only heterothallic Phytophthoras are to be found, contains the most variable strains, and these have become the source of greatest confusion in this genus. Many different strains of diverse morphological, physiological, and pathological characteristics mate with the greatest ease, as shown by the work of different investigators and by that of the writer (7). It matters very little whether or not we consider such unions as evidence for heterothallism or hybridism; the fact remains that the resulting oospores are likely to give rise to multitudinous organisms that will tax the ability and the patience of the orthodox morphologist. Add to this a ready tendency to dissociate and to give rise to still more strains possessing certain distinctions that cannot be ignored, and at once the complexity of the situation assumes a most acute aspect. It is pertinent to remark here that *P. parasitica* var. *rhei*, the one organism that dissociates with greatest abandon, is not heterothallic and will not mate with any of the oogonial or antheridial strains; consequently it does not seem advisable, at least in this case, to connect the dissociation phenomenon with heterothallism.

Because of such great variability of the *P. parasitica-P. palmivora* group, the safest way to identify the members of this group is by means of negative rather than positive characters; by what they are not and



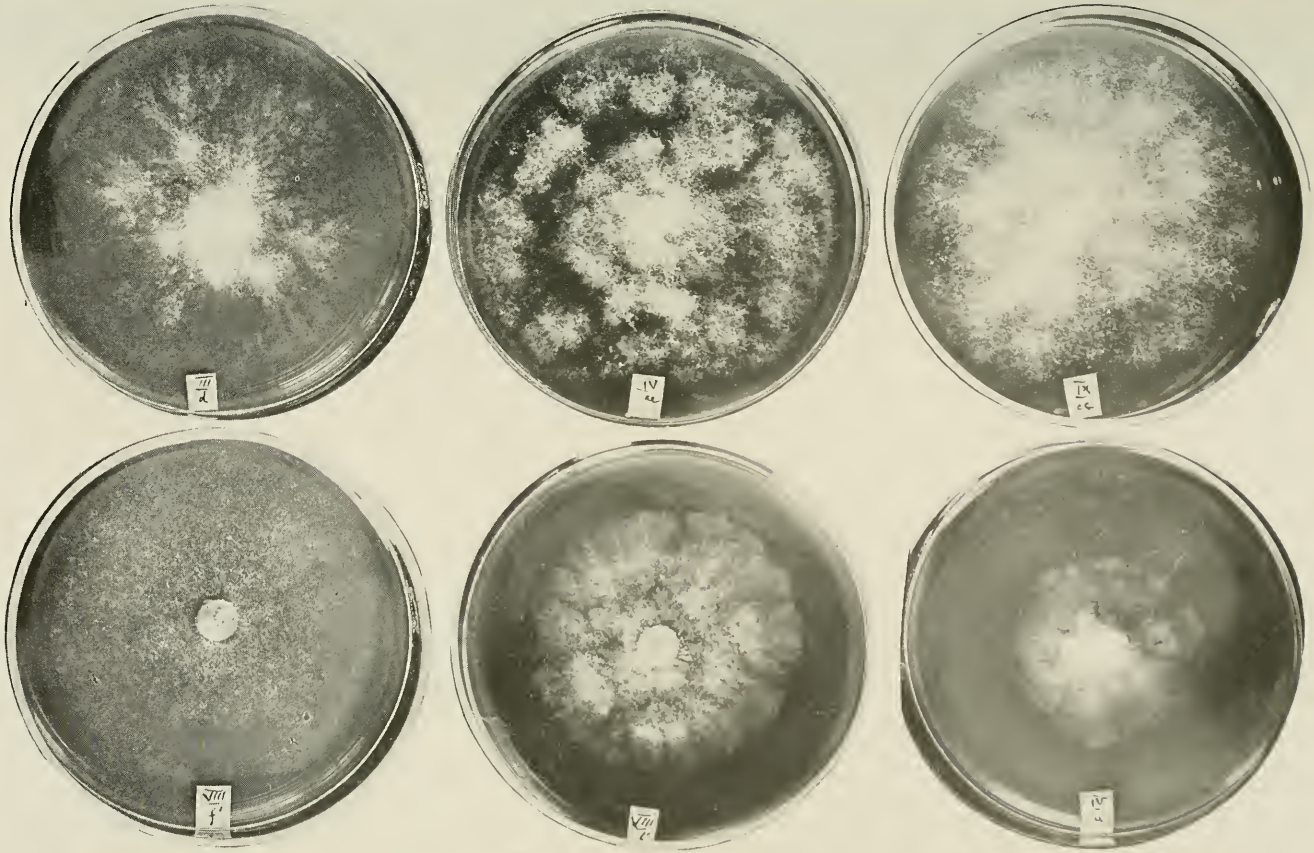


FIG. 1—Some representative dissociants of *P. parasitica* var. *rhei*.

do not, rather than by what they are and do. Even a casual perusal of the foregoing tables will reveal an astonishing plasticity of the group, the different strains and dissociants running the gamut of nearly all distinguishing characters with which other organisms are identified.

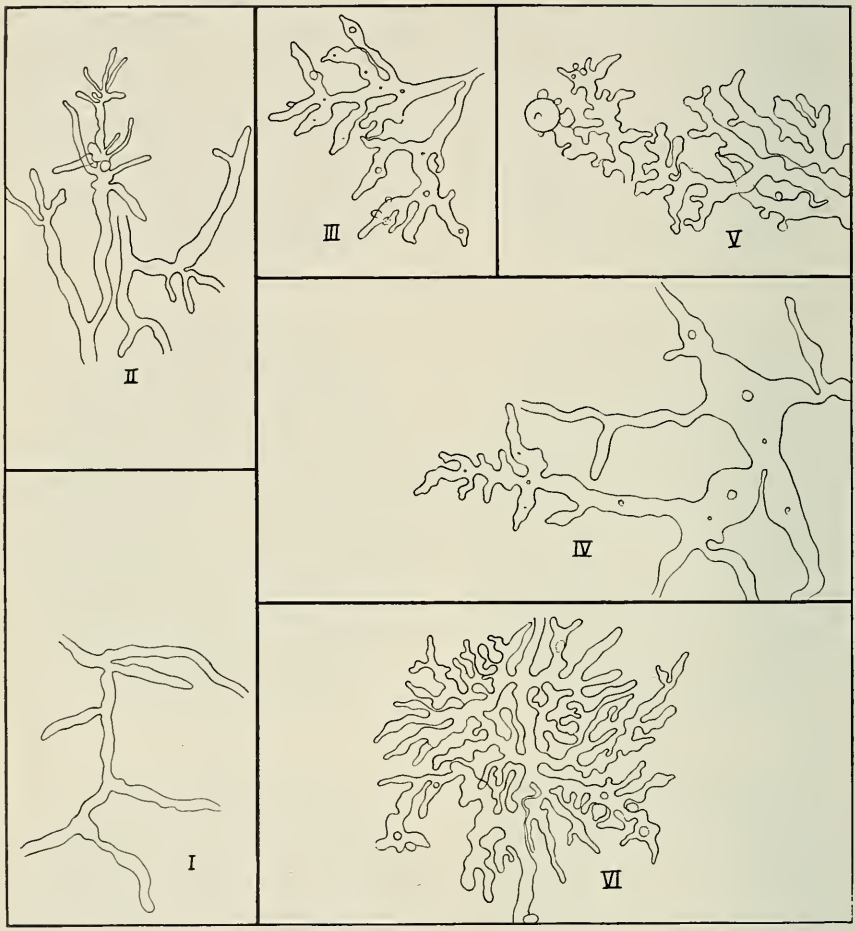


Fig. 2—Submerged hyphæ of the six dissociants of *P. faberi* 1 grown on malt-extract agar

Were it not for just a few reactions whereby all the members of this group show either positive or negative behaviors, a comprehensive classification would become a hopeless task. The inability of the group to give rise to sexual bodies in distilled water, and the ability to produce sporangia and chlamydospores regularly and in abundance, for instance, are of great help in identification work. On the other hand temperature

relationship, which has been greatly stressed, the pathogenicity of the members, the macroscopic and microscopic characters of different strains, and sexual relationships are so varied, so flexible and complex that their use in taxonomy of this species cannot be of any value.

While it is true that, in so far as our present knowledge goes, any heterothallic Phytophthora does, without doubt, belong to the *P. parasitica-P. palmivora* group of organisms, yet there are many homothallic, periodically homothallic and heterothallic, and neutral strains that also

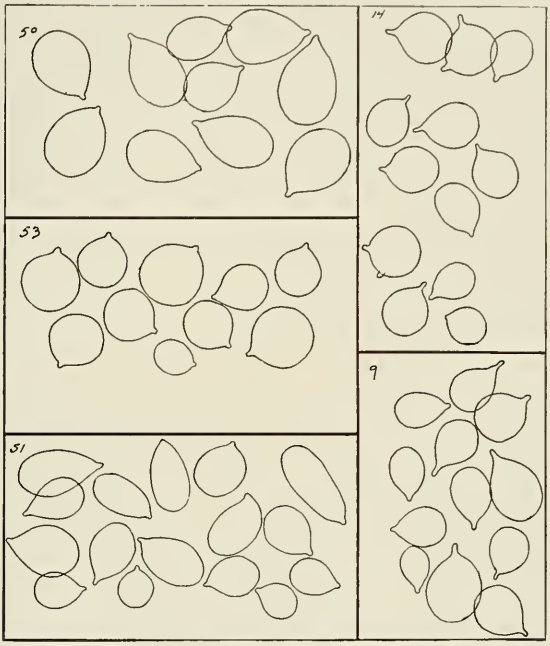


FIG. 3—Sporangia of the different dissociants of *P. parasitica rhei*. Note the differences in shape and size

belong to the same group. Pathogenicity is of still less value, the size and shape of chlamydospores altogether useless, and that of the sporangia not much better (figs. 3 and 4). Neither the ærial hyphæ nor the submerged (fig. 2) possess any distinctive characters except perhaps in the *P. infestans* group. When constantly faced by such extremes of variation, the investigator finds himself unable to evolve a scheme of classification based entirely or even largely upon morphological characters. The reluctance of many taxonomists to admit physiological reactions on equal footing with morphology is not based entirely on prejudice, because they, as well as the physiologists, realize that the same plasticity of protoplasm which works havoc with morphology also paralyzes many physiological characters. Such being the situation, the advisability of a reduced number of

species at once becomes apparent. It is true that to many persons a named species appears wrapped in a robe of sanctity, and all efforts to dethrone it are regarded as sacrilege; yet if we are to follow the dictum of common sense, we can readily see that any named species which cannot easily and definitely be identified fails to serve the purpose for which it was established. After all, the species as we conceive it does not exist outside our mind, for each organism is a separate entity and differs from every other individual by some known or unknown character. The degree and the constancy of this variation have yielded our present scheme of classification. For all practical purposes, therefore, it is the individual organism with which we are dealing and not the nebulous something which is known as the species. The plant pathologist finds little interest in a saprophytic strain of *P. parasitica*, yet a saprophytic strain of a parasite is of greater biological importance than the difference of a few microns between the sporangia of two different parasitic Phytophthoras.

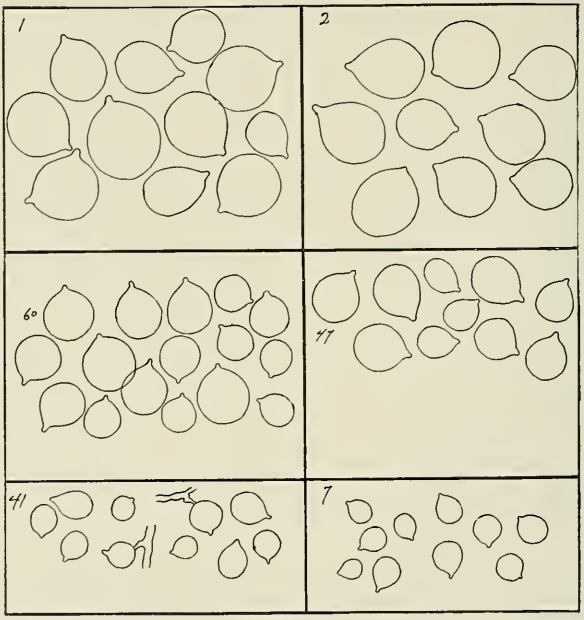


FIG. 4—Sporangia of different dissociants of *P. parasitica* var. *rhei*. Note the extreme variation in size

Tucker, Ashby, and others, in an effort to retain unaltered the status of type species, follow the practice of grouping the strains of a given species as typical or atypical. This serves no good purpose except to uphold a preconceived notion. The accident of a first discovery and description determines the typical strain, while a subsequent discovery and observation of another strain which in some respect, such as in the

shape of sporangia, may sharply differ from the original, determines the atypical strain. Thus nothing more tangible than a mere state of mind is brought forth to mould a plastic protoplasm. In reality there is no such thing as typical or atypical, but merely variability of living things. The writer does not wish to deny the continuity of the species, for there is, undoubtedly, a central axis around which the strains fluctuate and from which they rarely if ever break apart. The types which occur in greater frequency should constitute what has been termed typical, while those occurring less frequently should constitute the atypical. But since the word "atypical" signifies something aberrant, its use is not justifiable in this case. A given type may be found less frequently, yet just because it is not common, we are not justified in regarding it as aberrant. The case of *P. palmivora* illustrates how unsatisfactory it is to apply these terms to living things: this organism was first described as possessing sporangia much longer than broad, and any strain with more or less spherical sporangia was considered either atypical or a member of another species, *P. faberi*: but now that the latter species is merged with *P. palmivora*, typical or atypical sporangia can no longer be conceived. Nevertheless, we still find statements in the literature to the effect that growth habit, or temperature relationships, or pathogenicity, etc., are typical or atypical, the typical being considered the most important and the atypical often conveniently ignored.

EFFECT OF DISSOCIATION UPON TAXONOMIC CONCEPT

It has been seen that the numerous dissociants of *P. parasitica* var. *rhei* markedly differ in their morphology and behavior not only from other strains of *P. parasitica* but from one another as well. The differences in colony habit (fig. 1) immediately capture the eye. There is no similarity of pattern, no relationship whatever. Great differences exist in growth rate, in the presence or absence of aerial hyphæ, and in the gross morphology of the submerged hyphæ. The differences in the size of sporangia are startlingly numerous and conspicuous (figs. 3 and 4); the same thing applies to their shape. Differences in physiological behavior are no less conspicuous. Temperature relations, which have been given such an important place in the classification of Phytophthora as well as of other organisms, are so wide as to leave no doubt in the mind of the uninitiate that the organisms manifesting them belong to different species. And what of pathogenicity? We find the same wide gap among the different dissociants. For instance, 51 of the 90 dissociants of *P. parasitica* var. *rhei* rotted Grimes Golden apple, and the remaining 39 did not; similar results were obtained with Northwestern Greening. However, only 23 of the dissociants could rot the fruit of crab apple, *Pyrus coronaria*. In this connection it is interesting to note that before the arrival of the cold days in January, when the fallen fruits were still green, only ten of the dissociants were able to cause a rot. The inoculation experiments were repeated with rhubarb plants growing in pots in the greenhouse. Of all the dissociants only 25 produced wilt,

five of the organisms wilting and destroying the entire plant and twenty bringing about the wilt of only one or two leaves. The rhubarb plants belonged to the same variety. What happened to the pathogenicity of so many of the dissociants? It was not lost, but merely suppressed, coming to the fore again when the variants dissociated again or reverted back to their prototype. Obviously, therefore, pathogenicity is not a valuable taxonomic point in a group like *P. parasitica,* where there is no host specialization; but where such specializations do occur, its use is a fairly sound procedure.

Specific characters in many organisms, but particularly in Phytophthoras, are often very slender. When, therefore, certain dissociants tend to break away from the routine path of the species and reveal seemingly new forms or behaviors, we begin to wonder if it would not be advisable to classify such dissociants as new varieties; we may argue that here are actual instances of evolution occurring under our very eye. After all, most of us admit that in the evolution of things one prototype gave rise to many. If such new things arise in the laboratory, there is no reason why they should not be as valid as those appearing in nature. Such a reasoning would demand consideration were it not for the unstable nature of these dissociants. Some are extremely plastic and will manifest dissociation nearly every time a transfer is made; others will remain constant for a certain period, varying from a few months to a few years. Figure 5 illustrates this very well. Just why a dissociant should suddenly appear, remain "pure" for years, and suddenly revert to its prototype, disappear for years, and then manifest itself once more, is something that cannot yet be explained; yet the fact remains. Consequently any attempt to classify a given dissociant, no matter how widely different it may be from its prototype, may eventually lead to an anomalous situation. It would be very convenient to overlook such dissociants, but obviously it is impossible to do so. Even if one were to admit the baseless theory that the "artificial" conditions of laboratory alone are conducive to dissociation and that in nature no such things occur despite the fact that many so-called "natural" conditions do not at all best serve the needs of the fungus, we would still be faced by the same situation. Only rarely can a Phytophthora species be identified directly from the host; consequently pure-culture studies, with the resultant dissociative phases, become inevitable.

Before we can properly evaluate the effect of dissociation upon our taxonomic concept, it becomes necessary to crystallize our concept concerning dissociants and their relation to the strain and to the species. If we consider the strain as a component of the species, then the dissociant is a component of the strain. In other words a given dissociant, as seen by the investigator, does not appear and behave as a complete species but as a fragment of one because the dissociant expresses not all the phases of the species, but only some; others remain hidden and may manifest themselves only in the form of further dissociants. According to this scheme, therefore, the 90 dissociants of *P. parasitica rhei* collectively represent the strain, but individually they represent only fragments of

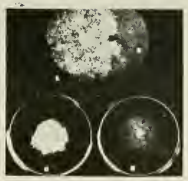


Fig. 5—The extreme right line of this diagram is the most significant one. Note that dissociant VII continued to "breed true" to type for many successive generations over a period of two years and then suddenly reverted back to the original type and continued to "breed true" for four years. At the end of that period, however, dissociant VII again made an appearance and continued very much as it did before. This shows how difficult it is to fix a given type

it—only some of the facets of a complex prism. All the characteristics which distinguish a given species of Phytophthora should theoretically be present in any individual representative of the species. In some representatives these are more constantly fixed. In others they are in a constant state of flux; hence the numerous dissociants sectoring away from a given culture. Just what controls the emergence and submergence of the specific characters and why some dissociate more, others less if at all, cannot be explained at present. But since such things do occur and very often quite constantly and abundantly, we are forced to the conclusion that one organism can give us but a partial picture of the species; that it is but a brick in the superstructure that is to become the species. Whether such bricks are furnished by dissociants or by additional strains, is relatively unimportant. The essential thing to consider is that the individual is no longer as valuable in giving us the species concept as it was formerly. Consequently a type specimen has no more value than any other specimen; the normal or the abnormal, the typical or the atypical are all considered as representative phases of the species and the workers need no longer concern themselves with artificial barriers which have hitherto hindered a clear concept. A first discovery and description has been allowed to impart a sanctified halo to the type specimen and has thus chained the species concept to a rigid cell. What right have we to establish a type based on one specimen, and later either relegate all other specimens which do not conform to this narrow concept to comparative neglect, or brand them with the stigma of atypical forms? What we need is a composite species built up with as many strains and dissociants as we can study. While such a scheme would by no means eliminate taxomic difficulties, it would greatly reduce them. Many organisms which would otherwise be considered either new species or new varieties would be found to belong to an old species. A species may be considered an authentic one when judged by the standard of "experts", but so long as it cannot be identified by keys and descriptive data at our disposal, it cannot have any value. Common sense rather than hair-splitting standards should be the criterion in such matters.

In the light of the foregoing statements, what is the effect of the 90 dissociants of *P. parasitica* var. *rhei* upon the taxonomic concept of the genus Phytophthora, with particular reference to the largest and the most cosmopolitan group represented by such organism as *P. palmivora, P. parasitica*, etc.? We find that many characteristics which formerly have been considered dependable for the separation of species are duplicated by one or more dissociants, which trace the path of the species and point to an ultimate and inevitable grouping together of many organisms hitherto considered distinct. Many different strains not related to the dissociants duplicate in their morphology and behavior the dissociants themselves; perhaps one may feel justified in making a new species out of a new and not well-known strain, but one would hesitate a long time before doing this in case of a dissociant the history of which, with reversions and further dissociations into newer variants, is well known to him. The chief value of the dissociants, therefore, lies in their known

performance-history. An organism cannot, in one phase of its life, be considered as one species, and an entirely different one in another phase of its history. It is possible that some of the dissociants may gradually become so fixed as rightfully to be considered a new species; otherwise we would expect no relationships between species and no evolutionary advances, but so long as data at our disposal fail to reveal a permanent fixity we must of necessity consider the composite behavior of all the dissociants and of all the strains as constituting the only authentic specific sphere. This, therefore, has been the criterion in the merging into one species of all the different organisms hitherto considered as new species or varieties.

Some of these listed below have had very scanty description and are not available in pure culture. Judging from what description is available, they undoubtedly belong to this group. Others have been merged or have been proposed to be merged in two different species by other workers as well as by the writer. In the light of the foregoing experiments as well as data available from other sources, all the following species and varieties are hereby merged with *Phytophthora palmivora* Butl.

P. allii Saw.
P. arecæ (Colem.) Pethyb.
P. carica Hara
P. faberi (Faber) Maubl.
P. fici Hori
P. jatrophæ Jensen
P. manoana Sid.
P. meadii MacRae
P. melongenæ Saw.
P. melongenæ var. *ananaphthoros* Sid.
P. mexicana Hots. and Hart.
P. nicotianæ Breda de Haan
P. parasitica Dast.
P. parasitica var. *rhei* Godf.
P. parasitica var. *nicotianæ* Tucker
P. symmetrica Sid.
P. tabaci Saw.
P. terrestris Sherb.
P. theobromæ Colem.

Such a treatment may seem a bit too drastic, but none of the foregoing organisms possesses a single character worthy of specific rank. If the foregoing 19 cultures were to be labeled only with a symbol and presented to any number of specialists for identification, there would be not one correct identification. If in addition to these one were to include all the dissociants and strains described in this paper, no self-respecting specialist would even attempt to separate them, notwithstanding all his familiarity with the fine points that are acquired with constant association. Whatever characteristics the foregoing nineteen organisms may possess, they can be duplicated by some strain or by some dissociant of

P. palmivora. Let us take the temperature factor, for instance: Tucker (*loc. cit.*) uses it in his key for the primary separation of *P. parasitica* from *P. palmivora.* Yet the writer's results, obtained under more nearly constant and accurate incubation conditions, do not uphold Tucker's results. Many of the dissociants of *P. parasitica* var. *rhei* grow at 35° C., to be certain, but 23 failed to grow at 32.5° C., and 12 made no growth even at 31° C. Of the six dissociants of *P. faberi* 1, only one failed to grow at 35° C., and five of them made some growth even at 37° C. *P. faberi* 3 and 4, and all six strains of *P. palmivora* except one, made some growth at 35° C. It is obvious, therefore, that the temperature factor is worthless in so far as its value in the separation of the strains classified under *P. parasitica* and *P. palmivora* is concerned. Other factors such as presence or absence of fruiting bodies and their morphology, host relations, etc. are of no more value than temperature relations. Finally, since heterothallic strains of *P. parasitica* readily mate with *P. faberi* or *P. palmivora* strains, the futility of the retention of *P. parasitica* as a definite species or even variety at once becomes apparent.

P. nicotianæ has been changed by Tucker to *P. parasitica* var. *nicotianæ* merely because of the ability of this fungus to infect tobacco. In the case of such an omnivorous group of organisms, host relationships cannot be considered of any value in taxonomy because they lead merely to the creation of a great many new varieties, a phenomenon of variation within the species which has already been discussed. Since there is no other characteristic whatever whereby this organism can be separated from other strains of the same group, the writer cannot recognize *P. parasitica* var. *nicotianæ* as valid and therefore merges it with *P. palmivora. Phytophthora mexicana,* likewise, does not possess any distinguishing characteristics whereby it can be separated. The strains named by Sideris, such as *P. manoana, P. melongenæ* var. *ananaphthoros,* and *P. symmetrica,* are so obviously mere representatives of the *P. parasitica* type of organisms that it is difficult to understand on what basis they were given specific or varietal ranks. The remaining organisms have been discussed by Tucker and the writer agrees with him concerning their lack of a specific status.

An analysis of the species which are retained by the writer is now in order; he wishes to repeat that the only reason why many of these "species" are retained is that they possess one or more apparently constant characteristics whereby they can be singled out from the rest. So long as newer strains or dissociants continue to uphold this stability there will be no cause to disarrange the present scheme, but as soon as exceptions arise, newer combinations will become necessary.

The organisms to be discussed are arranged in different groups not only for convenience but also because they possess a certain close relationship. The first one is termed *infestans* group and contains *P. infestans, P. phaseoli,* and *P. thalictri.* The second one is the *syringæ* group and may be divided into two sub-groups: the first sub-group, typified by paragynous antheridia, consists of *P. cactorum* and *P. cactorum applanata;* the second sub-group, characterized by amphigynous antheri-

dia, contains *P. megasperma, P. boehmeriæ, P. erythroseptica, P. cryptogeæ, P. richardiæ,* and *P. heveæ. Phytophthora erythroseptica* var. *atropæ* undoubtedly belongs here, but because of its position in the key it is associated with the next group, which is termed the *palmivora* group. This is similarly divided into two sub-groups: the first one contains *P. colocasiæ, P. cambivora,* and *P. erythroseptica* var. *atropæ* and is characterized by its extreme sensitiveness to malachite green; the second one is not so sensitive to the dye and contains *P. cinnamomi, P. drechsleri, P. capsici, P. citrophthora,* and *P. palmivora.*

A dependable specific character for one species may be entirely unreliable for another. Consequently morphological and physiological characters and host relationships have been freely used in some and have been disregarded in others. In case of the *infestans* group, for instance, host specialization is quite narrow, and the identification of *P. infestans, P. phaseoli,* and *P. thalictri* should offer no difficulty whatever. Add to this a very slowly-growing habit on certain agars as contrasted with the spreading growth made by all other species on similar agars, and any remaining doubt concerning a correct classification is at once eliminated. *Phytopthora infestans* may be sharply delimited because of the rareness of the sexual bodies. *P. phaseoli* and *P. thalictri* produce their sexual bodies in great abundance; in the case of the latter almost the entire culture seems to consist of oogonia and antheridia. In the next group of organisms *P. syringæ, P. hibernalis,* and *P. porri* are separated with equal ease from all others by their temperature limitations. Tucker believes that *P. hibernalis* is the same as *P. syringæ,* yet, whereas *P. hibernalis* forms its sexual bodies abundantly and with great ease when transferred from pea broth to distilled water, *P. syringæ* fails to form a single such body. Since this seems to be an easy way of separating it, the writer retains *P. hibernalis* as distinct from *P. syringæ. P. porri* also fails to form sexual bodies in distilled water, but since it has a comparatively greater temperature tolerance, it can be distinguished from *P. syringæ.*

The ability of the cactorum group to form sexual bodies after being transferred from pea broth to distilled water serves as a useful and dependable criterion in the separation of the organisms from all others. While a minimum period of three days after the transfer of fungus to distilled water will suffice to induce oogonia and antheridia, six days may prove more satisfactory. The chief essential for a ready development of the sexual bodies consists of the use of a vigorous but sterile mycelium. This is easily obtained by growing the organisms in deep culture dishes. Within four or five days after the initial transfer and at a temperature of 20°C. there will be a rich colony in all except perhaps *P. hibernalis, P. syringæ* and *P. porri,* the three closely-related and possibly similar species which might require a couple of days' additional growing period.

P. cactorum and *P. cactorum* var. *applanata* differ from the syringæ group by their greater temperature tolerance and from the remaining organisms of the *cactorum* group by their predominatingly paragynous

antheridia. *P. cactorum* var. *applanata* is readily separated from *P. cactorum* by its predominatingly non-papillate sporangia. *P. citricola* is undoubtedly *P. cactorum* as suggested by Tucker. The two unavailable and imperfectly described species, *P. cyperirotundati* and *P. lepironiæ*, may in all probability be included here, if previous "species" described by Sawada are any criteria.

Phytophthora megasperma possesses such large oogonia and oospores that there should be no reasonable doubt as to its status. *P. boehmeriæ* is readily separated from the remaining four organisms because it tolerates larger quantities of malachite green, whereas *P. erythroseptica, P. cryptogeæ, P. heveæ,* and *P. richardiæ* are extremely sensitive to this dye. *Phytophthora heveæ* is separated because of the fact that it does not grow at 8° C., while the others do. *P. erythroseptica* has decidedly larger oospores than either *P. cryptogeæ* or *P. richardiæ;* and while *P. cryptogeæ* grows at 31°C., *richardiæ* does not

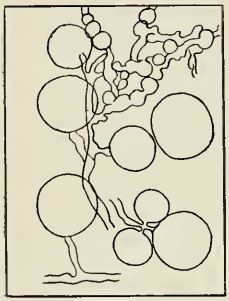


Fig. 6—Chlamydospores and hyphal swellings of *P. cinnamomi*

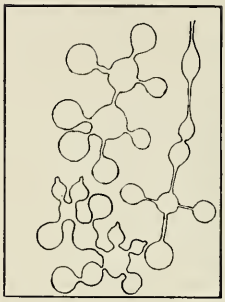


Fig. 7—Hyphal swellings on *P. drechsleri*. Under the low power of the microscope these appear like closely-packed spheres, often forming considerable patches

The following members of the palmivora group, *Phytophthora colocasiæ, P. cambivora,* and *P. erythroseptica* var. *atropæ,* are extremely sensitive to malachite green, while the remaining are not. *P. colocasiæ* is papillate and the pedicels remain attached to the sporangia. Furthermore, it fails to grow at 8°C. *P. cambivora* and *P. erythroseptica* var. *atropæ* are usually without papillæ and pedicels, and are able to grow at 8°C. Whereas *P. cambivora* does not produce oogonia and antheridia, *P. erythroseptica* var. *atropæ* does.

In the second sub-group of organisms, *P. cinnamomi* is readily recognized by its typical hyphal swellings, by its chlamydospores, and by its lack of sporangia particularly on solid media (Fig. 6). According to Mehrlich* *P. cinnamomi* does not form sporangia when the mycelium is transferred to distilled water, but in soil infusion (Hawaiian soil) such bodies form readily and abundantly. By employing special treatment both Rands and Tucker have induced the formation of sporangia. No such bodies have formed for the writer under the conditions outlined here. Of the remaining four organisms *P. palmivora* is the only one which forms both sporangia and chlamydospores; no chlamydospores have been observed in *P. drechsleri* (Fig. 7), *P. capsici,* and *P. citrophthora. Phytophthora drechsleri* is the only one of these three capable of

* Oral communication.

growing at 37°C. Finally, *P. capsici* is separated from *P. citrophthora* by its ability to give rise to oogonia and antheridia in oatmeal agar tubes, whereas no such bodies have been found in *P. citrophthora*. Curzi's *P. hydrophila* may well be merged with *P. capsici* as Tucker has suggested

According to the foregoing discussion 22 organisms can be identified without the use of any complicated media or apparatus, and consequently in the key which is to follow, all these organisms have been treated as bonafide species or varieties. But as stated before, the writer has prepared the key merely for the convenience of those who must attach a name to a given organism which they happen to isolate or study. In reality, however, the great majority of these organisms consist of no more than well-defined strains and as such manifest too many overlapping characteristics. *P. infestans*, *P. phascoli*, and *P. thalictri*, for instance, are distinguished from each other only by their host specialization, as morphologically they are similar. The rareness of oogonia in *P. infestans* and their abundance in *P. phaseoli* and *P. thalictri* can be considered no more specific than host specializations. Once we unreservedly admit that these are acceptable distinctions in the separation of species, there will be no end of "new species".

P. hibernalis, *P. syringæ*, and *P. porri* are very similar both morphologically and physiologically. All three organisms form both paragynous and amphigynous antheridia; the differences in the sizes of sporangia are neither great nor constant; the non-papillate nature of the sporangia holds for all three; and finally, temperature tolerance is not distinctive enough. So long as there are not very many strains for study and comparison, the differences as used in the following key are useful enough; but if experience with other and more common species may be taken as a criterion, it is probable that sooner or later these three organisms will be merged.

The jump from the foregoing three to *P. cactorum* and *P. cactorum* var. *applanata* is not at all a jump, but a mild transition. The only valid difference lies in the temperature relationships of the two groups. A temperature of 31°C. seems to be the upper limit for *P. cactorum*. Growth at this temperature is poor, and one strain does not grow at all. None made a growth for the writer at 32.5°C. The maximum temperature for *P. syringæ* is below 25°C.; that for *P. porri* is between 25°C. and 27°C. While the latter fungus failed to grow at 27°C., it remained alive and grew again when it was removed to 20°C. Thus with the upward trend of *P. porri* and the downward trend of *P. cactorum* 4 it is not at all unlikely that the boundaries of the two groups will meet and merge when more strains are isolated and studied. *Phytophthora cactorum* var. *applanata* with its non-papillate sporangia eliminates another barrier on the path of a future merger.

Next in order come *P. megasperma*, *P. boehmeriæ*, *P. erythroseptica*, *P. cryptogeæ*, *P. richardiæ*, and *P. heveæ*. The gap between these and *P. cactorum* is not a large one. Amphigynous antheridia predominating in the foregoing six organisms and paragynous antheridia predominating in *P. cactorum* are the chief morphological difference. Yet

these are not absolute; on the contrary, quite variable. We always qualify such specific differences by the word "predominatingly", otherwise an anomalous situation would follow. But is this a true specific character? Are we justified in separating two species on the clumsy difference of relative abundance of one type or another? This is doubtful. As concerns the differences in the size of oospores, we find a gradual transition and overlapping of boundaries. But so long as no other species can show oospores averaging 41 microns, *P. megasperma* may readily be considered distinct. On the other hand, *P. erythroseptica, P. cryptogeæ, P. heveæ, P. richardiæ,* and *P. erythroseptica* var. *atropæ* are alike in so many ways and unlike in so few that their common origin can readily be seen. If we had ten or twenty different strains of each of these, all the apparent dissimilarities might disappear. *Phytophthora boehmeriæ* and *P. megasperma* do not bear very close morphological resemblance to the other six organisms; in this respect they are still in need of connecting links.

Phytophthora colocasiæ possesses long, slender sporangia and persistent pedicels, yet many strains of *P. palmivora* also have long and slender sporangia. *P. capsici* and *P. mexicana*, as shown by the writer *(8)*, develop persistent pedicels when grown on pepper. Carne has described and illustrated his strain of *P. hibernalis* as possessing long and persistent pedicels. The extreme sensitivity of *P. colocasiæ* to malachite green is the chief distinction whereby it can be separated from *P. palmivora*, and its inability to form sexual bodies in distilled water is the most valid mark of separation from the preceding group. Yet *P. erythroseptica* var. *atropæ*, undoubtedly a strain of *P. erythroseptica*, also fails to form oogonia in distilled water. And while *P. cryptogeæ* and *P. richardiæ* do form such bodies, they show a transitional stage towards *P. erythroseptica* var. *atropæ* in that they require a longer period for their formation and that their oogonia and antheridia form scantily.

If *P. cinnamomi* produced sporangia on solid media or in distilled water, it would undoubtedly be placed with *P. palmivora*. In this connection it should be remarked that a number of strains of *P. palmivora* tend greatly to decrease their sporangia in favor of chlamydospores; sometimes the number of sporangia produced is so limited as to be negligible. Thus *P. palmivora* reaches into the boundaries of *P. cinnamomi. Phytophthora drechsleri, P. capsici*, and *P. citrophthora* are separated from *P. palmivora* by not possessing any *chlamydospores* and from *P. cinnamomi* by their ability to produce *sporangia*. *P. drechsleri* forms very few sporangia, thus approaching *P. cinnamomi;* a lack of well-defined papillæ renders this relationship still closer. It is true that *P. drechsleri* tolerates higher concentrations of malachite green and higher temperatures, yet such differences can hardly be specific in view of the fact that inconstant reactions abound in Table 2, where the strains of the same species often show entirely different growth responses. Similar instances are plentiful in the dissociants of *P. parasitica* var. *rhei*. As concerns the absence of chlamydospores in some, we again find that a number of strains of *P. palmivora* and some of the dissociants restrict

chlamydospores and thus invade the specific sphere of *P. drechsleri, P. capsici,* and *P. citrophthora,* the three species in which no true chlamydospores have been observed. The latter does not form any sexual bodies, yet numerous strains of *P. palmivora* also fail to form such bodies. Thus the separation between *P. citrophthora* and *P. palmivora* becomes a very thin and fragile one. The same thing applies to the difference between *P. capsici* and *P. citrophthora* on the one hand, and *P. capsici* and *P. palmivora* on the other.

In the light of the foregoing discussion the writer is inclined to think that some time in the future so many of the present-day species will be discarded that there will be no more than two or perhaps three firmly established species: viz., *P. infestans, P. cactorum,* and *P. palmivora.* In the meantime, however, the writer has retained all the species and varieties that can be identified with reasonable ease and certainty.

The merging of some additional species, particularly *P. parasitica,* with *P. palmivora* necessitates a further emendation of the species as follows:

Phytophthora palmivora is a widely distributed and cosmopolitan species of omnivorous habit; extremely variable both morphologically and physiologically. On ordinary media containing the essential salts, sugar, and organic nitrogen the colonies make a spreading growth, giving rise to numerous types of colonies varying from a smooth-combed to plumose and grumose types. Aerial hyphæ abundant, scanty, or absent; submerged hyphæ smooth and of even diameter, or uneven, gnarled, or bulbous. The maximum temperature tolerance varies from 30 to 37.5°C. Sporangia typically papillate, greatly variable in size and in form; chlamydospores spherical to subspherical, terminal or intercalary; both sporangia and chlamydospores develop readily and abundantly when a well-fed mycelium is transferred to distilled water. Sexual bodies present or absent in oatmeal agar tubes; antheridia typically amphigynous; homothallic, heterothallic, and neutral strains present. No sexual bodies developed when a well-fed mycelium is transferred from pea broth to distilled water. Sizes of oogonia and oospores variable; parthenogenetic oogonia may develop abundantly. In rare cases some cultures may approach sterility. Acid and base tolerance, as well as ability to endure malachite green and other toxic substances, extremely variable.

KEY FOR IDENTIFICATION OF PYTHOPHTHORA SPECIES

No growth on malt extract agar after 6 days at 20° C.
- Parasitic only on Solanaceæ and Scrophulariaceæ; oospores almost always absent, or if present, extremely rare — 1. *P. infestans*
- Parasitic only on *Phaseolus lunatus;* oospores abundant — 2. *P. phaseoli*
- Parasitic only on Thalictrum species — 3. *P. thalictri*

Good growth on malt extract agar after six days at 20°C.
- No growth at 27°C.
  - Sterile hyphæ form sexual bodies after being transferred from pea broth to distilled water — 4. *P. hibernalis*
  - Sterile hyphæ form no such bodies
    - Cultures killed at 27°C. after an exposure of 7 days — 5. *P. syringæ*
    - Cultures not killed — 6 .*P. porri*
- Growth at 27°C.
  - Sterile hyphæ form sexual bodies after being transferred from pea broth to distilled water
    - Antheridia predominatingly paragynous
      - Sporangia papillate — 7. *P. cactorum*
      - Sporangia not papillate — 8. *P. cactorum* var. *applanata*
    - Antheridia predominatingly amphigynous
      - Oospores average 41 microns — 9. *P. megasperma*
      - Oospores average 31 microns or less
        - Growth in presence of 1:8,000,000 malachite green — 10. *P. boehmeriæ*
        - No growth in presence of 1:8,000,000 malachite green
          - Growth at 8°C.
            - Growth at 31°C.
              - Oospores 31 microns — 11. *P. erythroseptica*
              - Oospores 24 microns — 12. *P. cryptogeæ*
            - No growth at 31°C. Oospores 24 microns — 13. *P. richardiæ*
          - No growth at 8°C. — 14. *P. heveæ*
  - Sterile hyphæ form no sexual bodies after being transferred from pea broth to distilled water
    - No growth in presence of 1:8,000,000 malachite green
      - No growth at 8°C.; sporangia papillate and pedicellate — 15. *P. colocasiæ*
      - Growth at 8°C.; sporangia not pappillate and not pedicellate
        - No sexual bodies formed in oatmeal agar — 16. *P. cambivora*
        - Sexual bodies formed in oatmeal agar — 17. *P. erythroseptica* var. *atropæ*
    - Growth in presence of 1:8,000,000 malachite green
      - No sporangia formed when sterile mycelium is transferred from pea broth to distilled water
        - Chlamydospores and hyphal swellings formed; no growth at 37°C. — 18. *P. cinnamomi*
      - Sporangia formed when sterile mycelium is transferred from pea broth to distilled water
        - No chlamydospores produced
          - Growth at 37°C.; sporangia usually rare and nonpapillate — 19. *P. drechsleri*
          - No growth at 37°C.; sporangia abundant and papillate
            - Sexual bodies formed in oatmeal agar tubes — 20. *P. capsici*
            - No such bodies formed — 21. *P. citrophthora*
        - Both chlamydospores and sporangia formed when sterile mycelium is transferred from pea broth to distilled water; sexual bodies in oatmeal agar tubes present or absent — 22. *P. palmivora*

SUMMARY

All available species and varieties of Phytophthora have been studied in order to obtain additional data as to their status in the genus.

A number of cultures have freely dissociated, particularly *P. parasitica* var. *rhei*, from which some 90 dissociants were separated and studied.

Five different temperatures, five different concentrations of malachite green, one concentration of tartaric acid, and one of potassium carbonate were used.

The ability of a given organism to produce sporangia, oogonia, and chlamydospores, either together or in different associations, was found to be a valuable criterion in classification.

Data resulting from the foregoing experiments were combined with dependable data obtained by other workers as well as by the writer and were utilized in the preparation of a taxonomic key.

Twenty-two species and varieties can be identified by the key.

A number of organisms have been merged together and a few have been reestablished in the preparation of the key.

The foregoing 22 organisms have been retained not because they are believed to have sound specific basis, but because they can be identified by the key.

The writer believes that there are not more than three good species in Phytophthora: viz., *P. infestans*, *P. cactorum*, and *P. palmivora*.

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